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PATTERNS OF STOPOVER BY WARBLERS DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

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Abstract.—Migrant warblers mist netted on Appledore Island, Maine, during spring and fall migration in 1990 and 1991 allowed analysis of seasonal differences in stopover patterns, including recapture rates, stopover lengths, and changes in mass and fat during stopover. Northern Waterthrushes (*Seiurus noveboracensis*) and American Redstarts (*Setophaga ruticilla*) had higher recapture rates in the fall than in the spring on Appledore Island. The Ovenbird (*Seiurus aurocapillus*) and the Canada Warbler (*Wilsonia canadensis*) had significantly longer stopovers in the fall than in the spring. During fall migration, young Northern Waterthrushes were more likely to be recaptured than adults, and young American Redstarts had longer stopovers than adults. During spring migration, female Magnolia Warblers (*Dendroica magnolia*) were more likely to be recaptured than males. Higher numbers of both male and female American Redstarts were recaptured in the fall than in the spring. American Redstarts, Northern Waterthrushes, and Ovenbirds showed no significant increase in fat class in the spring, while exhibiting significant increases in fat class in the fall. These three species also exhibited significant increases in mass during fall migration, while only the Ovenbird significantly increased mass in the spring. These data suggest that migrants show species, age, and sex specific seasonal differences in stopover pattern as well as differences in mass and fat accumulation. Such differences are likely affected by hormone titer, risk of predation, seasonal/temporal changes in weather patterns, and/or differences in food availability. Moreover, stopover sites may be used differently as a result of seasonal differences in relation to ecological barriers as well as distances to either breeding or wintering grounds. *Received 28 April 1993, accepted 20 April 1994.*

Few researchers have investigated differences in the stopover biology of migratory passerines between spring and fall migration (e.g., Rappole and Warner 1976; Cherry 1982; Safriel and Lavee 1988; Winker et al. 1992a, b, c; Weisbrod et al. 1993), and none of these studies was conducted along the western North Atlantic Ocean. Moreover, studies comparing age and sex differences in the stopover biology within species are few in number (e.g., Ellegren 1991, Lavee et al. 1991). Because patterns of passerine migration differ between seasons (Rappole and Warner 1976, Yom-Tov 1984) and timing of migration differs between age and sex groups (Francis and Cooke 1986, Ellegren 1991), patterns of stopover behavior may also differ among these groups and seasons.

In the spring, migrants presumably must arrive at breeding sites early to establish quality territories, but not so early as to risk mortality, from

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inclement weather, predation, or inadequate food supply (Francis and Cooke 1986). Fall migrants must leave in time to find adequate food supplies and favorable weather for their migration, and are faced with competition both enroute to and on their wintering grounds. Spring migrants face the same pressures but have the added requirement of returning early enough to secure productive breeding territories. This would be particularly true of males (Francis and Cooke 1986) and for this reason we expect shorter stopovers and fewer recaptures of migrants, especially males, in spring than in fall. Also one might predict that lean birds should remain longer at stopover sites than those with sufficient energy reserves. This prediction particularly is logical for spring migrants who are close to their final destination.

In this study we attempted to answer the following questions (1) Do migrant species exhibit different patterns of stopover during spring and fall migration? (2) Do age and sex classes have different patterns of stopover between seasons? (3) Are the fat classes of migrants arriving on Appledore Island different between seasons? and (4) Do migrants experience similar changes in fat class and mass during stopover between seasons?

STUDY SITE AND METHODS

We mist netted warblers on Appledore Island, Maine (42°58′N 70°36′W), a 33.6-ha island in the Gulf of Maine (Fig. 1). Appledore is the largest island in the Isles of Shoals, a group of nine small islands and several ledges 14.5 km southeast of Portsmouth, New Hampshire, and 9.7 km from the nearest point of the mainland. While most of the islands are sparsely vegetated with much of their area composed of exposed rock, Appledore has a variety of vegetation types. Lyman (1988) estimates that one-third of Appledore's area is exposed rock, with the remaining two-thirds divided into vegetation of four types (1) upland meadow and low shrubs, characterized by grasses, forbs, rose (*Rosa virginiana*), poison ivy (*Rhus radicans*), goldenrod (*Solidago* sp.), choke cherry (*Prunus virginiana*), and raspberry (*Rubus* sp.); (2) interior low-lying areas of high shrubs including winterberry (*Ilex verticillata*), apple (*Pyrus* sp.), and pin cherry (*Prunus pensylvanicus*); (3) disturbed areas covered mainly with grasses, forbs, sumac (*Rhus typhina*), and poplar (*Populus* sp.); and (4) wetland areas characterized by cattails (*Typha latifolia*), rushes (*Scirpus* sp. and *Juncus* sp.), iris (*Iris versicolor*), grasses and smartweed (*Polygonum* sp.). Upland meadows and low shrubs and interior areas of high shrubs comprise approximately 37% and 45% of the vegetated areas of the island, respectively (Lyman 1988). Appledore is the only island in the Isles of Shoals with available fresh water.

We captured birds between 18 May and 8 June in 1990, 15 May–6 June in 1991 (3545 total net-h), 16 August–20 September in 1990, and 16 August–21 September in 1991 (5877.5 total net-h). Weather permitting, we operated six to ten mist nets (12 × 2.6 m, 30 mm mesh) during most of the daylight hours, with the mist nets opened just before sunrise, closed around sunset, and checked approximately every 30 min throughout the day. We banded birds with U.S. Fish and Wildlife Service bands as they were brought to a central location. For each bird captured (and recaptured), we recorded age and sex, the degree of skull pneumatization, unflattened wing chord (0.5 mm), fat class (see below), and mass (0.01 g).

FIG. 1. Map of the New England coast showing the location of the Isles of Shoals (courtesy of the Shoals Marine Laboratory).

In the case of recaptures, we did not refer to the initial data sheets, so that measurements were not influenced by information previously recorded. The fat classification system we use is similar to that described by Cherry (1982). Because only a few individuals were assigned fat classes of 3 or 4 each season (3.9% overall, N = 2770), we included birds with a fat class of 3 or 4 with the individuals in fat class 2 in our analysis.

We calculated minimum length of stopover by subtracting the initial date of capture from the date of last recapture (Cherry 1982, Moore and Kerlinger 1987, Ellegren 1991). Thus, a one-day stopover refers to a stopover of one night and part of two days. This method differentiates between passage migrants, birds that interrupt migration only during the day but presumably continue migration that night, and stopover migrants, birds that suspend migration for at least one night. This method resulted in a conservative estimate of the time a migrant remained at the site because we could not assume that the date of initial capture

was the first day of a stopover nor could we assume that the final recapture occurred on the last day of a stopover (Cherry 1982, Biebach et al. 1986, Moore and Kerlinger 1987). Average stopover lengths would be biased if residents as well as migrants of the same species were included in the analysis. Thus we excluded Common Yellowthroats (*Geothlypis trichas*) and Yellow Warblers (*Dendroica petechia*) from this analysis because they are confirmed regular breeders on Appledore Island (Borror and Holmes 1990).

When comparing mass between initial capture and subsequent recaptures, mass must be taken at the same time of day (Rappole and Warner 1976) or corrected to the same time of day (Cherry 1982, Moore and Kerlinger 1987, Loria and Moore 1990). We corrected mass to 12:00 DST for all individuals by computing the average percent mass gain per hour using individuals captured more than 5 h apart on the same day (Moore and Kerlinger 1987, Loria and Moore 1990). Migrant warblers had an average hourly mass gain of 0.210 ± 0.401% (N = 51 individuals). We computed an individual's mass change by subtracting the initial mass from the final mass.

In many passerine species, males tend to be larger than females, and adults tend to be larger than young birds. Males also often have longer wing chords than do females. To compare increases in mass, we calculated the percent gain during stopover using the following formula: percent gain = (final mass − initial mass)/initial mass × 100%. Daily increases in mass were calculated by dividing the percent gain by stopover length. This method reduces the possibility of sex or age related size differences influencing observed differences in mass.

Significance levels of statistical tests between spring and fall denote one-sided probabilities to reflect our expectation of fewer recaptures and shorter stopovers in the spring. Because we expected increases in fat class and mass during stopover, tests on fat and mass changes were also one-sided. All other statistical tests reflect two-sided probabilities. In the case of two sample *t*-tests, we did not assume equal variance and therefore we present results using degrees of freedom corrected for unequal variance.

RESULTS

During 1990 and 1991, we banded 3412 birds of 69 species during spring migration and 2723 individuals of 82 species during fall migration. We present results here from the 1722 migrant warblers captured during spring migration and the 1048 migrant warblers captured during fall migration (Table 1).

Migrants were more likely to be recaptured in the fall than in the spring. Only the Magnolia Warbler (scientific names in Table 1) had a higher recapture rate in the spring than in the fall, but this particular difference between seasons was not statistically significant (Table 2). Migrant warblers also tended to stop longer during fall migration than during the spring. Although most species tended to have longer stopovers in the fall than in the spring (Table 3), only the Ovenbird and the Canada Warbler differed significantly in this regard (Mann-Whitney *U*-test, $U = 72.5$, $P = 0.016$; and $U = 6.0$, $P = 0.026$, respectively). Within the Parulinae, we found significantly different stopover lengths between species in the fall (Kruskal-Wallis test, $t = 13.97$, $P = 0.03$). However, in the spring,

TABLE 1

CAPTURES BY SEASON (1990–1991) OF WARBLER SPECIES WITH MORE THAN 10 INDIVIDUALS CAPTURED ON APPLEDORE ISLAND, MAINE

	Spring			Fall		
	N	Date range[a]	Median	N	Date range[a]	Median
Blue-winged Warbler (*Vermivora pinus*)	0	—	—	33	228–254	239
Tennessee Warbler (*V. peregrina*)	6	139–144	141	9	234–254	246
Nashville Warbler (*V. ruficapilla*)	7	138–158	145	17	229–260	252
Northern Parula (*Parula americana*)	33	136–152	141	6	252–264	258–9
Chestnut-sided Warbler (*Dendroica pensylvanica*)	34	136–157	145	38	228–261	239
Magnolia Warbler (*D. magnolia*)	578	136–159	146	51	232–264	252
Cape May Warbler (*D. tigrina*)	1	141	—	56	229–263	251
Black-throated Blue Warbler (*D. caerulescens*)	40	136–155	140	21	239–261	250
Black-throated Green Warbler (*D. virens*)	12	136–156	144	8	229-262	251
Blackburnian Warbler (*D. fusca*)	32	136–158	151	5	238–261	254
Prairie Warbler (*D. discolor*)	0	—	—	15	228–256	233
Bay-breasted Warbler (*D. castanea*)	20	139–152	146–7	15	240–263	252
Blackpoll Warbler (*D. striata*)	122	136–159	147	56	228–264	255
Black-and-white Warbler (*Mniotilta varia*)	44	136–153	141	59	228–261	240
American Redstart (*Setophaga ruticilla*)	337	135–159	148	176	228–262	251
Ovenbird (*Seiurus aurocapillus*)	79	136–158	144	51	228–261	243
Northern Waterthrush (*S. noveboracensis*)	70	136–159	144–5	233	228–261	245
Mourning Warbler (*Oporornis philadelphia*)	53	145–159	152	44	228–259	240
Wilson's Warbler (*Wilsonia pusilla*)	33	136–152	140	62	229–260	246
Canada Warbler (*W. canadensis*)	177	137–158	149	47	229–264	239
Yellow-breasted Chat (*Icteria virens*)	0	—	—	26	234–262	248–9

[a] Earliest and latest Julian date of capture.

TABLE 2

COMPARISON OF RECAPTURE RATES DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Spring N	Spring Percent recaptured	Fall N	Fall Percent recaptured	χ^2	*P*
Magnolia Warbler	676	1.78%	51	0.00%	1.00	0.320
Blackpoll Warbler	122	0.00%	56	3.57%	4.41	0.036
Black-and-white Warbler	44	6.82%	59	15.25%	1.74	0.187
American Redstart	337	3.18%	176	13.64%	21.54	0.001*
Mourning Warbler	53	1.89%	44	9.09%	2.55	0.110
Ovenbird	79	8.86%	51	25.49%	6.58	0.010
Northern Waterthrush	70	2.86%	233	17.60%	9.60	0.002*
Canada Warbler	177	1.69%	47	4.26%	1.12	0.291
Total	1722	2.26%	1048	11.07%	95.59	0.000*

* Significant at $\alpha = 0.05$ after sequential Bonferroni correction for multiple tests.

individual species did not differ significantly in the average length of stopover ($t = 9.28$, $P = 0.10$).

The age ratio of individuals captured between seasons was not significantly different ($\chi^2 = 2.28$, df = 1, $P = 0.131$). During spring migration, young birds (hatch-year individuals in the fall and second-year individuals in the spring) comprised 93.9% of the individuals captured (N = 1271), and in the fall young birds accounted for 92.4% of the individuals captured (N = 1047; Table 4). Young American Redstarts and Ovenbirds

TABLE 3

COMPARISON BETWEEN SEASONS OF THE MEAN MINIMUM LENGTH OF STOPOVER ON APPLEDORE ISLAND, MAINE

Species	Spring N[a]	Spring Mean[b]	Spring Range[c]	Fall N[a]	Fall Mean[b]	Fall Range[c]
Magnolia Warbler	12	2.6 ± 2.1	1–7	0	—	—
Chestnut-sided Warbler	0	—		4	1.5 ± 1.0	1–3
Black-and-white Warbler	3	5.7 ± 5.0	1–11	9	4.1 ± 5.0	1–17
American Redstart	12	2.6 ± 1.5	1–6	24	3.4 ± 3.8	1–18
Ovenbird	7	2.4 ± 1.0	1–4	13	5.1 ± 2.8	1–13
Northern Waterthrush	2	6.0 ± 0.0	6	41	4.3 ± 3.3	1–16
Canada Warbler	3	1.0 ± 0.0	1	2	3.0 ± 1.4	2–4
Total	39	2.9 ± 2.2	1–11	116	3.9 ± 3.4	1–18

[a] Number of individuals recaptured.
[b] Mean and standard deviation of stopover length in days.
[c] Range of stopover length in days.

TABLE 4

COMPARISON OF PROPORTION OF YOUNG INDIVIDUALS CAPTURED DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Spring		Fall	
	N[a]	Percent young	N[a]	Percent young
Magnolia Warbler	492	95.9%	51	90.2%
Chestnut-sided Warbler	31	93.6%	38	97.4%
Blackpoll Warbler	102	97.1%	56	83.9%
Black-and-white Warbler	36	100.0%	59	96.6%
American Redstart	245	81.6%	176	90.9%
Mourning Warbler	20	100.0%	44	97.7%
Ovenbird	24	100.0%	51	98.0%
Northern Waterthrush	13	100.0%	232	87.1%
Canada Warbler	161	99.4%	47	95.7%
Total	1124	93.7%	754	91.1%

[a] Number of individuals that could be aged (based on age keys in Pyle et al. [1987]).

were more likely to be recaptured in the fall than in the spring (χ^2 = 13.1, df = 1, $P < 0.001$: χ^2 = 3.13, df = 1, P = 0.036, respectively). Young Northern Waterthrushes were more likely to be recaptured than adults during fall migration (χ^2 = 2.87, df = 1, P = 0.045). During fall migration, young American Redstarts had significantly longer stopovers than adults (U = 10.0, P = 0.03).

The sex ratios of individuals captured during spring and fall migration were essentially equal (χ^2 = 0.0, df = 1, P = 0.99). Females accounted for just over 51% of the individuals captured in both seasons (Table 5).

TABLE 5

COMPARISON OF RECAPTURES BY SEX FOR FOUR SPECIES OF WARBLERS DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Females				Males			
	Spring		Fall		Spring		Fall	
	N[a]	Percent recaptured	N[a]	Percent recaptured	N[a]	Percent recaptured	N[a]	Percent Recaptured
Magnolia Warbler	267	3.3%	19	0.0%	300	0.3%	24	0.0%
Black-and-white Warbler	38	7.9%	32	18.8%	7	0.0%	27	11.1%
American Redstart	160	3.8%	79	15.2%	217	2.7%	93	11.8%
Canada Warbler	110	2.7%	29	3.5%	66	0.0%	17	5.9%

[a] Number of individuals recaptured.

TABLE 6
COMPARISON OF FAT CLASS DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

Species	Spring		Fall	
	N	Percent lean[a]	N	Percent lean[a]
Magnolia Warbler	578	52.6%	51	84.3%
Chestnut-sided Warbler	38	70.6%	34	52.6%
Blackpoll Warbler	122	11.5%	56	82.1%
Black-and-white Warbler	44	34.1%	59	22.0%
American Redstart	377	62.6%	175	66.9%
Mourning Warbler	53	66.0%	44	45.5%
Ovenbird	79	40.5%	50	30.0%
Northern Waterthrush	68	32.4%	232	22.0%
Canada Warbler	177	84.2%	46	71.7%

[a] Percentage of individuals in fat class 0 or 0.5.

Both female and male American Redstarts were more likely to be recaptured during fall migration than during spring migration (females: $\chi^2 = 9.94$, df = 1, $P \leq 0.001$; males: $\chi^2 = 10.32$, df = 1, $P \leq 0.001$). Female Magnolia Warblers were more likely to be recaptured than males during spring migration ($\chi^2 = 7.22$, df = 1, $P = 0.007$). No differences in proportion of individuals recaptured by sex were detected during fall migration in any species.

Six species were leaner during spring migration than during fall migration and only three species were leaner in the fall (Table 6). Magnolia Warblers captured in the spring were significantly fatter than those captured in the fall ($\chi^2 = 19.06$, df = 1, $P \leq 0.001$). Likewise, Blackpoll Warblers captured during the spring were significantly fatter than those captured during the fall ($\chi^2 = 85.78$, df = 1, $P \leq 0.001$). Small sample sizes did not allow a comparison of initial fat class of individuals captured only once with that of recaptured individuals.

A pattern of no significant change in fat class during the spring and significant increases in fat class in the fall was found in American Redstarts (spring: $Z = 1.155$, $P = 0.124$; fall: $Z = 2.758$, $P = 0.003$), Northern Waterthrushes (spring: $Z = 0.447$, $P = 0.328$; fall: $Z = 2.985$, $P = 0.002$), and Ovenbirds (spring: $Z = 1.414$, $P = 0.079$; fall: $Z = 2.081$, $P = 0.019$; Fig. 2).

Migrants stopping over in the fall gained significantly more mass, as a percentage of initial mass, than migrants stopping in the spring ($t = 2.64$, df = 77.7, $P = 0.01$; Table 7). We found similar patterns of higher mass gains in the fall than in the spring in Ovenbirds ($t = 2.19$, df =

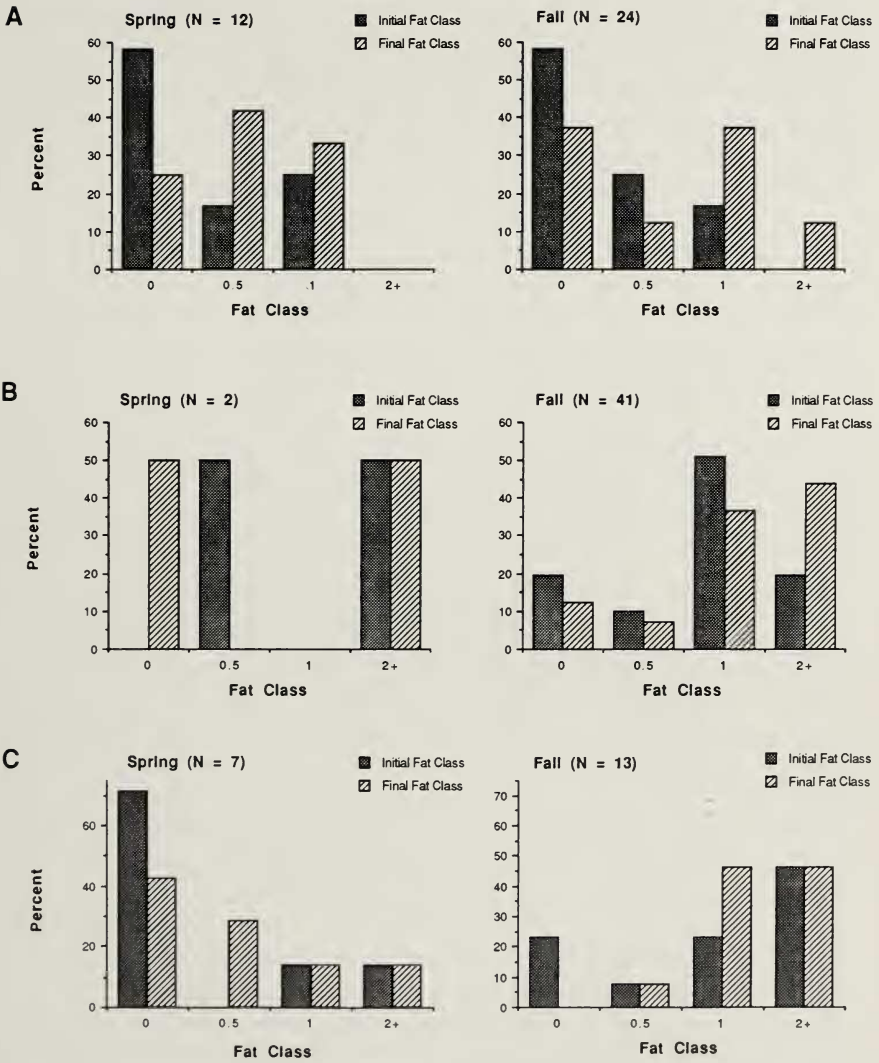

FIG. 2. Changes in the distribution of fat classes between initial and final capture by migrants stopping over on Appledore Island, Maine. A. American Redstart. B. Northern Waterthrush. C. Ovenbird.

15.7, $P = 0.044$) and American Redstarts ($t = 2.30$, df = 30.2, $P = 0.029$).

Paired t-tests on the difference between initial and final mass further assessed the change in body mass during each season. All migrants com-

TABLE 7

COMPARISON OF WEIGHT CHANGES BY WARBLERS DURING SPRING AND FALL MIGRATION ON APPLEDORE ISLAND, MAINE

	Spring			Fall		
	N[a]	Percent increase[b]	Daily percent increase[c]	N[a]	Percent increase[b]	Daily percent increase[c]
Magnolia Warbler	12	2.5 ± 9.3	−1.3 ± 5.1	0		
Chestnut-sided Warbler	0			4	5.9 ± 8.1	3.0 ± 3.0
Blackpoll Warbler	0			4	−2.1 ± 6.2	−2.1 ± 6.2
Black-and-white Warbler	3	11.9 ± 17.2	1.3 ± 4.6	9	6.6 ± 11.5	1.5 ± 3.6
American Redstart	12	0.5 ± 7.1	−0.5 ± 3.8	24	7.2 ± 10.3*	1.1 ± 4.7
Ovenbird	7	3.8 ± 4.1	1.4 ± 1.7	13	12.4 ± 13.1*	1.8 ± 1.9*
Northern Waterthrush	2	1.3 ± 10.6	0.2 ± 1.8	41	8.1 ± 8.6*	2.6 ± 2.7*
Canada Warbler	3	1.1 ± 6.4	1.1 ± 6.4	2	−8.2 ± 10.3	−2.2 ± 2.4
Total	39	2.5 ± 8.4	−0.1 ± 2.5	116	6.9 ± 10.0*	1.7 ± 3.5*

[a] Number of individuals recaptured.
[b] Percent gain = (100 × final mass − initial mass)/initial weight.
[c] Daily percent gain = (100 × final mass − initial mass)/initial weight)/length of stopover.
* Significance at $\alpha = 0.05$ level after sequential Bonferroni correction for multiple *t*-tests between weight change and zero.

bined exhibited significant mass increases during both seasons (spring: $t = 1.90$, df = 38, $P = 0.033$; fall: $t = 7.35$, df = 115, $P < 0.001$). The Ovenbird was the only species that experienced a significant average increase in mass during the spring ($t = 2.47$, df = 6, $P = 0.024$). In the fall, Ovenbirds ($t = 3.42$, df = 12, $P = 0.003$), Northern Waterthrushes ($t = 6.03$, df = 40, $P \leq 0.001$), and American Redstarts ($t = 3.43$, df = 23, $P = 0.001$) experienced significant increases in mass.

Because migrants tend to have longer stopovers in the fall than in the spring we also compared daily percent increases between the seasons. Migrants stopping over on Appledore Island gained a significantly higher percentage of mass on a daily basis in the fall than in the spring ($t = 2.59$, df = 58.5, $P = 0.012$; see Table 7). During spring migration, migrants did not exhibit daily percent increases in mass ($t = -0.19$, df = 38, $P = 0.854$). However in the fall, daily percent increases in mass were significant ($t = 5.38$, df = 115, $P < 0.001$). Migrants showed no significant difference in daily mass gain between species in either the spring or the fall (spring: $F_{5,32} = 0.50$, $P = 0.773$; fall: $F_{6,88} = 1.56$, $P = 0.168$).

DISCUSSION

Differences in stopover behavior may be influenced by a number of factors, including distance left to travel during migration (Bairlein 1985, Moore and Kerlinger 1987), time in the annual cycle (Lavee et al. 1991), initial energetic condition (Cherry 1982, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Loria and Moore 1990, Kuenzi et al. 1991), location of a stopover site in relation to an ecological barrier (Moore and Kerlinger 1987, 1991; Winker et al. 1992a), and suitability of a stopover site, including adequacy of a food supply and competition (Hansson and Pettersson 1989, Kuenzi et al. 1991, Moore and Yong 1991, Moore and Simons 1992). These factors may result in differences in stopover patterns (differences in recapture rates and observed lengths of stopover) not only between seasons but between species and even between individuals and sexes. Although we discuss the data here from the standpoint of single factor analysis, we are aware that certain factors may be additive or confounding in their effects on migration.

We observed different patterns of stopover on Appledore Island between spring and fall migration, both in terms of the proportion of individuals recaptured and length of stopover. Although in this study we encountered more migrant warblers during spring migration (Table 1), both in overall numbers and in terms of individuals captured per net-h, the fall migration yielded more American Redstart and Northern Waterthrush recaptures and longer stopovers in Ovenbirds and Canada Warblers (Tables 2 and 3). Although these results are similar to those of Rabol and

Petersen (1973) in Denmark and Lavee et al. (1991) in the Sinai, Rappole and Warner (1976) reported higher recapture rates in spring than in fall migration for several passerine species (e.g., Nashville Warbler, Ovenbird, and Mourning Warbler) stopping along the Gulf coast. Both distance from the initial point of departure (Abramsky and Safriel 1980) and distance to final destination (Bairlein 1985, Moore and Kerlinger 1987) have been suggested as factors affecting the probability of stopover by migrants. The warbler species encountered on Appledore Island have breeding ranges which extend into New England and Canada. While the northernmost wintering grounds of some migrant warblers are in southern Florida, winter ranges for all of the Appledore migrants extend into central America and the West Indies or South America. Furthermore, although several species have breeding grounds which extend into the southern United States (e.g., Black-and-white Warbler, Ovenbird, and American Redstart), individuals encountered on Appledore Island are most likely breeding in New England or eastern Canada. Therefore, migrants captured during spring migration are farther from their point of initiation of spring migration (at least 1700 km away) than they are to their final destination (which could be 10 to 200 km away). Likewise, migrants captured on Appledore Island during fall migration are closer to the point of initiation than they are to their final destination. The higher recapture rates of American Redstarts and Northern Waterthrushes and longer stopovers of Ovenbirds and Canada Warblers on Appledore in the fall indicate that migrants may exhibit more stopover behavior (e.g., more recaptures and longer stopover periods) early in migration and close to the point of migration initiation. However, the location of a stopover site in relation to an ecological barrier may be as important as its location relative to breeding and wintering grounds.

Appledore Island is positioned at the edge of a major ecological barrier, the Atlantic Ocean. The nearest point of land is only 10 km away and lies directly north (Fig. 1). During fall migration, migrants encountering Appledore Island are assumed to be headed south and thus will see only water. Therefore, migrants must either prepare for barrier crossing or reorient in some way, perhaps by returning to the coastline. During spring migration, northbound migrants encountering Appledore can still see land in their seasonally correct direction, north, and thus may not be likely to interrupt migration by an extended stopover. Spring migrants also may be continuing movement north without undertaking true migratory flights to find suitable food sources and less competition. Movements similar to this were reported by Riddiford and Auger (1983) in Kent. Such movements would result in a lower perceived proportion of individuals exhib-

iting stopovers because individuals would not be recaptured but may have flown the 10 km to the mainland without continuing migration.

A significant finding of this study related to age groups was the high proportion of young birds captured in the spring. Although high proportions of young birds have been documented along the coast in the fall (Baird and Nisbet 1960, Drury and Keith 1962, Murray 1966, Morris 1993), similar ratios heretofore have not been documented in the spring. Because inland stations have lower percentages of young migrants (regularly 60–75%) compared to coastal stations, Ralph (1981) suggests that high proportions of young individuals (90% or more) may indicate the periphery of a species' migratory route. Following this rationale, the high percentage of young individuals captured on Appledore Island during the spring may indicate that most migratory routes are farther inland. A notable exception to the above pattern is the American Redstart which had a much lower proportion of young individuals captured than other species (Table 4). This increased proportion of adults in the population could indicate that during spring migration American Redstarts are following a different migratory path than most other migrant warblers in the northeast. Such a difference in their migratory path could result either from their flying northward and staying along the coast or from their following an inland route north and then changing their heading to the northeast to reach northeastern breeding grounds.

Differences also exist between adults and juveniles during fall migration. Young Northern Waterthrushes were more likely to be recaptured and young American Redstarts had longer stopovers than adults in the fall. The higher recapture rates and longer stopovers among young birds compared to adults in this study are consistent with Ellegren's (1991) study of Bluethroats (*Luscinia s. svecica*) in Sweden. Drury and Keith (1962) suggested that a high percentage of young birds along the coast could be due to hesitation or indecision by young birds encountering a large body of water compared to the continuation of migration over water by adults. This suggestion may in part explain the difference in recaptures and stopover lengths as well. An alternative explanation for the longer stopovers by young birds might be that young birds are not physiologically prepared to initiate a barrier crossing; however, small samples did not permit examination of this hypothesis.

Data presented here indicate a seasonal difference in patterns of stopover between the sexes of Magnolia Warblers. The results show that during spring migration females were significantly more likely to be recaptured than males, but in the fall, there was no significant difference in the rate of recapture between the sexes. Stopovers of several days would result in a delayed arrival at the breeding grounds compared to other

individuals migrating at the same time. Because males often arrive at breeding grounds before females to obtain and establish quality territories (Francis and Cooke 1986), males may be more motivated to continue migration in the spring than females. However, in the fall both sexes may have the same priorities, as both males and females of many species of migrant warblers defend winter territories against all conspecifics (Rappole and Warner 1980). The reported absence of a significant difference in the probability of stopover between the sexes in any species of warblers in the fall may reflect these similar priorities.

Blackpoll Warblers and Magnolia Warblers captured on Appledore were significantly leaner in the fall than in the spring. These results differ from the findings of other studies. Studying trans-Saharan migrants in the Sinai, Safriel and Lavee (1988) found that most migrants were fat-depleted in the spring, and that mass/wing length ratios tended to be lower in the spring than in the fall. Biebach (1985) and Gwinner et al. (1988) suggest that the suppression of migratory restlessness, and thus the probability of stopover, are critically affected by both the energetic conditions of a migrant and the possibility of increasing mass at that stopover site. Therefore, one would expect to recapture more migrants with low fat stores than migrants with high fat stores. At this site, Blackpoll Warblers were leaner in the fall than in the spring and a higher proportion (and more individuals) of this species were recaptured on Appledore Island in the fall.

Our results indicate that migrant warblers tend to increase fat stores and mass during stopover on Appledore Island during both spring and fall migration, but these increases are significant only in the fall (Fig. 2 and Table 7). Data presented here also show that migrants gain significantly more mass during stopovers on Appledore in the fall than in the spring. Bibby and Green (1983) and Moore and Kerlinger (1987) suggest that significant increases in mass by migrants is an indication that an area is a suitable stopover site. Additionally, Winker et al. (1992b, c) and Weisbrod et al. (1993) have shown that habitat use by migrants during stopovers differs seasonally. Therefore, differences in the mass and fat changes between seasons may indicate that the shrub habitats of Appledore Island provide a suitable stopover site for American Redstarts, Ovenbirds, and Northern Waterthrushes in the fall, but in the spring, food may be less available and competition may be increased.

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